

# ANNALE

UNIVERSITEIT VAN STELLENBOSCH

VOLUME 36 SERIE A NO. 8 (1961)

## CONTRIBUTIONS TO THE CRANIAL MORPHOLOGY OF PSEUDOTRITON RUBER RUBER (SONNINI)

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(With 11 text-figures)

Thesis accepted for the Master's Degree in Science  
in Zoology at the University of Stellenbosch

Submitted: June, 1960

## ABSTRACT

The cranial morphology of *Pseudotriton ruber ruber* is described. An outstanding feature is the absence in the ethmoidal region of both a processus praenasalis inferior lateralis and a processus praenasalis superior medius. Other outstanding features are the fusion of the premaxillaries with each other, the lack of a sclerotic cartilage and the fact that the posterior part of the septomaxillary invades the cartilage bordering the fenestra narina. The sound-conducting apparatus consists of a columella and an operculum; the latter is fused to the footplate of the former, and the opercular portion is in synchondrotic union with the ventral rim of the fenestra ovalis. This condition is regarded as primary. An epihyal is probably present and the jaw suspension is amphistylic. The skull is also monimostylic and akinetic, owing to the immovability of the pars quadrata palatoquadrati.

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## INTRODUCTION

According to most modern classifications, the family *Plethodontidae* includes 17 genera.

The generic name, *Pseudotriton*, was instituted by Tschudi (1838). The species known at present as *Pseudotriton ruber ruber*, also commonly known as the Northern Red Salamander (Bishop, 1943), was first described by Sonnini in 1802 as *Salamandra rubra*. Cope (1889) failed to recognize it as belonging to the genus *Pseudotriton*, and in his description he placed it under the genus *Spelerpes*, instituted by him; he named it *Spelerpes ruber*. In 1917 Stejneger and Barbour (quoted from Stejneger and Barbour, 1923) placed it in the genus *Eurycea*, as *Eurycea rubra rubra*. Dunn (1920) finally recognized it as belonging to the genus *Pseudotriton* and altered its name to *Pseudotriton ruber ruber*. Stejneger and Barbour (1923) accepted Dunn's identification. The generic name *Spelerpes* is no longer recognized.

## MATERIAL AND TECHNIQUE

The material used for this investigation consisted of two adult specimens, a male and a female, obtained from two American dealers. The male specimen measured 60.5 mm. from snout to vent and 100 mm. from the snout to the tip of the tail. Corresponding measurements for the female specimen were 73 mm. and 114.5 mm. respectively. The specimens were fixed in 10% formalin, and decalcified in a 6% solution of concentrated  $\text{HNO}_3$  in 70% alcohol. Standard microtechnical methods were employed in preparing transverse sections of the heads of both female and male at  $12\mu$  and  $15\mu$  respectively. The  $12\mu$  sections were stained with azocarmine and counter-stained with azan solution. The  $15\mu$  sections were stained with Mayer's acid haemalum and counter-stained with van Gieson's stain.

Graphic reconstructions were made from projection drawings of transverse sections according to a method devised by Pusey (1939).

## THE OLFATORY CAPSULE

In the ethmoidal region a septum nasale is absent. Anteriorly its place is taken by the cavum internasale (fig. 2), and posteriorly by the tectum internasale and the planum internasale (figs. 4 and 5). The cavum internasale houses the glandula intermaxillaris (figs. 3 and 4). Similar conditions obtain in *Triturus* (De Beer, 1937), *Onychodactylus japonicus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954). In *Siren lacertina* (Wiedersheim, 1877) a cavum internasale is absent because the trabeculae fuse to form a complete septum nasale. The absence of the cavum internasale in *Salamandra maculosa* (De Beer, 1937) is probably due to the same cause.

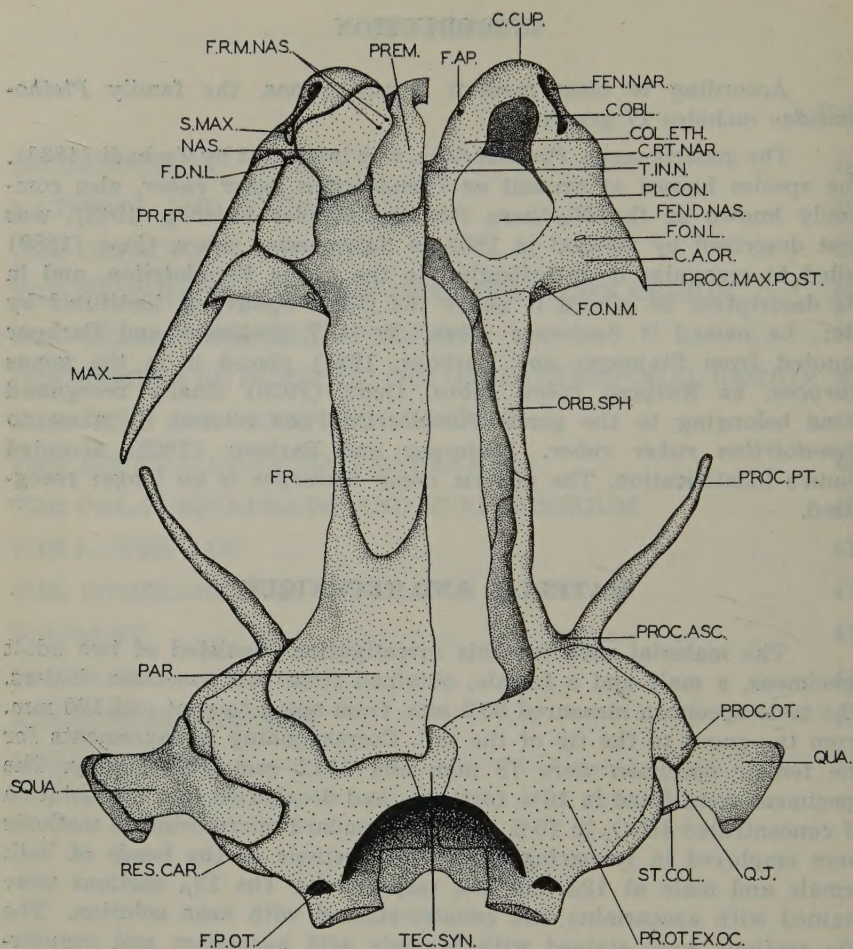


Figure 1.

Graphic reconstruction of the skull x10.1 approx. Dorsal view. C.A.OR. cartilago antorbitalis; C.CUP. cartilago cupularis; C.OBL. cartilago obliqua; COL.ETH. columella ethmoidalis; C.RT.NAR. cartilago retronarina; F.AP. foramen apicale; F.D.N.L. foramen ductus nasolacrimalis; FEN.D.NAS. fenestra dorsalis nasi; FEN.NAR. fenestra narina; F.O.N.L. foramen orbitonasale laterale; F.O.N.M. foramen orbitonasale mediale; F.P.OT. foramen postoticum; FR. frontal; F.R.M.NAS. foramen for ramus medialis nasi V(a); MAX. maxillary; NAS. nasal; ORB.SPH. orbitosphenoid; PAR. parietal; PL.CON. planum conchale; PREM. premaxillary; PR.FR. prefrontal; PROC.ASC. processus ascendens; PROC.OT. processus oticus; PROC.MAX.POST. processus maxillaris posterior; PROC.PT. processus pterygoideus; PR.OT.EX.OC. prootic-exoccipital complex; Q.J. quadratojugal; QUA. quadrate; RES.CAR. residual cartilage; S.MAX. septomaxillary; SQUA. squamosal; ST. COL. stylus columellae; TEC. SYN. tectum synoticum; T.IN.N. tectum internasale.

The cavum internasale in *Pseudotriton* is bounded antero-dorsally by the processus praenasales of the premaxillaries (fig. 1), and the tectum internasale (figs. 1, 3 and 4) forms a short cartilaginous roof over its posterior portion. Ryke (1950) found that the tectum internasale



in *Onychodactylus japonicus* stretches very far anteriorly, whereas in *Diemictylus* (Chung, 1931) it is absent. The cavum internasale is laterally bounded by the medial walls of the nasal capsules, which are posteriorly connected by the planum internasale thus forming its posterior wall (fig. 5). Ventrally the cavum internasale is incompletely bounded by the antero-ventrally situated fused portion of the premaxillaries and by the vomers which fail to meet in the middle line (fig. 2). The cavum internasale of some urodeles, such as *Megalobatrachus japonicus* (Aoyama, 1930), *Cryptobranchus* and *Amphiuma* (Jarvik, 1942), is incompletely divided by a median unpaired cartilago infranasalis. The latter author regards the cartilage in question as a vestige of the internasal ridge of the *Porolepiformes*.

Peter (1898) maintains that the lower urodeles possess a septum, whereas the higher ones have a cavum internasale instead. Since Gaupp (1906) found that in *Cryptobranchus alleghaniensis* there is a cavum internasale but no intermaxillary gland, Stadtmüller's (1936) contention that the presence of a cavum internasale in some urodeles is dependent upon the presence of the intermaxillary gland, appears to be untenable.

An unpaired processus praenasalis superior medius, as reported for *Salamandra maculosa* (Parker, 1879), *Onychodactylus fischeri* and *Hynobius* (Chung, 1931), *Chioglossa* (Stadtmüller, 1936) and *Onychodactylus japonicus* (Ryke, 1950), is absent, as in *Diemictylus* (Chung, 1931), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954).

The antero-medially projecting processus praenasalis inferior lateralis, arising from the ventro-medial surface of the cartilago cupularis of *Siren* (Parker, 1877), *Triturus* and *Hynobius* (Chung, 1931), *Salamandra* (Francis, 1934), *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954), is entirely lacking in *Pseudotriton ruber ruber*, which, in this respect, agrees with *Megalobatrachus japonicus* (Aoyama, 1930). It is very small in *Diemictylus*, *Pseudosalamandra* and *Hynobius* (Chung, 1931).

The short, thick planum internasale is posteriorly confluent with a transversely situated cartilage, presumably the lamina praecerebralis, separating the cavum internasale from the cavum cranii (fig. 5). This condition is similar to that of *Salamandra* (Francis, 1934), *Chioglossa* and *Desmognathus* (Stadtmüller, 1936), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). However, in *Triturus* (Born, 1876; Wiedersheim, 1877), *Diemictylus* (Higgins, 1920; Stadtmüller, 1936), *Euproctus* (Stadtmüller, 1936), and *Onychodactylus japonicus* (Ryke, 1950) a fenestra praecerebralis is present, and the cavum cranii and the cavum internasale are only separated by the ectomeninx. Aoyama (1930) found signs of degeneration in the cartilago internasalis (presumably the lamina praecerebralis, according to his description) in both larval and adult stages of *Megalobatrachus*, although a fenestra praecerebralis is never formed. The nervus olfactorius enters the nasal capsule through the foramen olfactorium, which is dorsally bounded by the columella ethmoidalis and ventrally by the planum internasale (figs. 5 and 6).

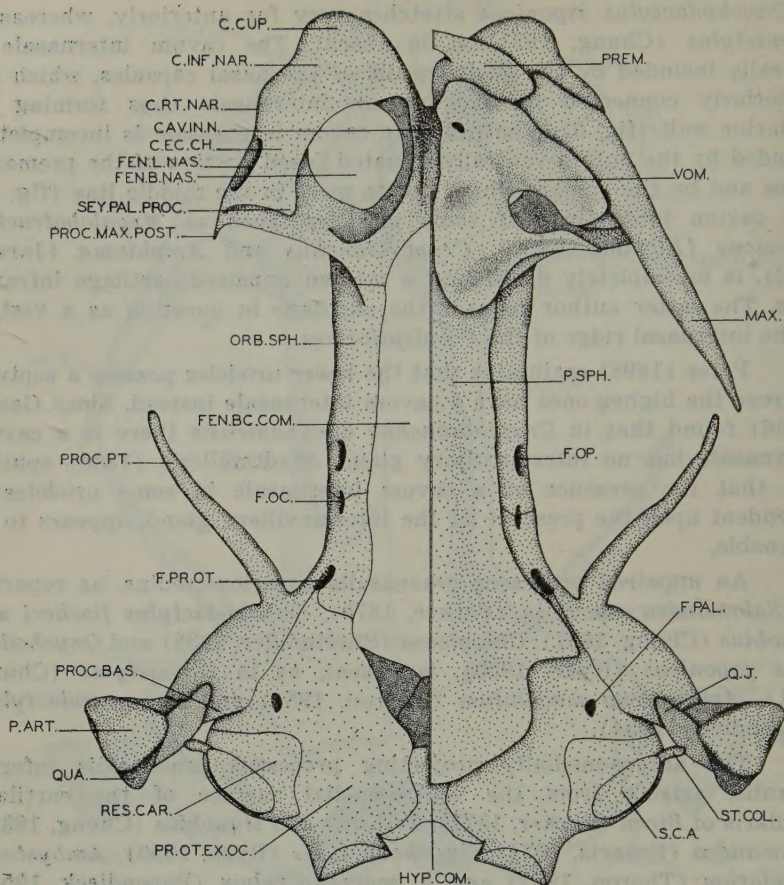


Figure 2.

Graphic reconstruction of the skull  $\times 10.1$  approx. Ventral view. CAV. IN.N. cavum internasale; C.CUP. cartilago cupularis; C.EC.CH. cartilago ectochoanalis; C.INF.NAR. cartilago infranarina; C.RT.NAR. cartilago retronarina; FEN.BC.COM. fenestra basicranialis communis; FEN.B.NAS. fenestra basalis nasi; FEN.L.NAS. fenestra lateralis nasi; F.O.C. foramen oculomotorium; F.OP. foramen opticum; F.PAL. foramen palatinum; F.PR.OT. foramen prooticum; HYP.COM. hypochordal commisure; MAX. maxillary; ORB.SPH. orbitosphenoid; P.ART. pars articularis; PREM. premaxillary; PROC.BAS. processus basalis; PROC.MAX.POST. processus maxillaris posterior; PROC.PT. processus pterygoideus; PR.OT.EX.OC. prootic-exoccipital complex; P.SPH. parasphenoid; Q.J. quadratojugal; QUÁ. quadrate; RES.CAR. residual cartilage; S.C.A. sound-conducting apparatus; SEY.PAL.PROC. Seydel's palatal process; ST.COL. stylus columellae; VOM. vomer.

The comparatively large fenestra dorsalis nasi is medially bounded by the columella ethmoidalis, anteriorly by the cartilago cupularis, antero-laterally by the cartilago obliqua, postero-laterally by the planum conchale and posteriorly by the cartilago antorbitalis (fig. 1). Through the fenestra dorsalis nasi pass bloodvessels and nerve fibres of the



ramus medialis nasi V(a) (fig. 5). Higgins (1920) regards the formation of the fenestra dorsalis nasi in urodeles as secondary, since he could demonstrate resorption of the planum tectale during ontogeny. Stadtmüller (1936) and Jarvik (1942) fully agree with the above-mentioned statement. Chung (1932) found that in *Hynobius* the tectum nasi is more complete in the larval stage than in the adult.

The fenestra narina (fenestra endonarina communis, Jarvik, 1942) is situated antero-laterally to the fenestra dorsalis nasi and separated from it by the cartilago obliqua (fig. 1). The fenestra narina is anteriorly bounded by the cartilago cupularis, posteriorly by the somewhat twisted cartilago retronarina which separates it from the fenestra lateralis nasi, and ventro-laterally by the cartilago infranarina (lamina nario-choanalis, Jarvik, 1942) which separates it from the fenestra basalis nasi (fig. 2). The slit-like external naris is situated in the anterior part of this antero-posteriorly elongated fenestra narina. The glandula nasalis externa is located in its posterior part. The ductus nasolacrimalis runs dorsally to the prefrontal, pierces it anteriorly, then runs dorsally to the planum conchale and finally enters the nasal capsule through the fenestra narina, behind the septomaxillary (figs. 1, 3 and 4). *Plethodon* (Lapage, 1928) shows a deviation from the normal urodele condition, as the apertura nasalis externa is separated from the ductus nasolacrimalis by a cartilaginous bar. Jarvik (1942) therefore distinguishes between a fenestra endonarina anterior for the apertura nasalis externa and a fenestra endonarina posterior for the ductus nasolacrimalis.

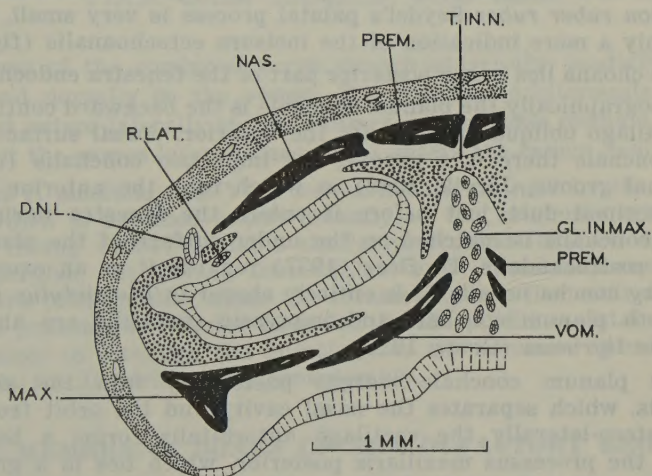


Figure 3.

Transverse section through the region of the tectum internasale. D.N.L. ductus nasolacrimalis; GL.IN.MAX. glandula intermaxillaris; MAX. maxillary; NAS. nasal; PREM. premaxillary; R.LAT. ramus lateralis nasi V(a); T.IN.N. tectum internasale; VOM. vomer.

The fenestra lateralis nasi (fenestra retronarina, Jarvik, 1942) is situated behind and ventro-laterally to the fenestra narina (fig. 2); being separated from it by the broad cartilago retronarina. It is dorsally bounded by the planum conchale and ventrally by the cartilago

ectochoanalis as in *Diemictylus*, *Hynobius retardatus*, *H. naevis* and *Onychodactylus japonicus* (Chung, 1931), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). In *Onychodactylus fischeri* and *Hynobius nebulosus* (Chung, 1931) the fenestra lateralis nasi is absent, but Fox (1959) reports a rudimentary fenestra lateralis nasi in the nasal capsule of larval *Hynobius nebulosus*. The fenestra lateralis nasi houses the lateral bulge of the nasal sac (so-called Jacobson's organ). Jarvik (1942) regards the fenestra lateralis nasi as an entirely new formation caused by the lateral bulge of the nasal sac.

The large fenestra basalis nasi (fenestra endochoanalis, Jarvik, 1942) is situated ventrally in the solum nasi (fig. 2). Its anterior border is formed by the dome-shaped cartilago cupularis. Antero-laterally it is bounded by the cartilago infranarina, laterally by the cartilago ectochoanalis and Seydel's palatal process, which is, however, not very prominent. Medially it is bordered by the medial capsular wall (trabecula). It would appear that in all urodeles there is an incisure of varying size between Seydel's palatal process and the lateral wall of the nasal capsule. This incisure was called the incisura ectochoanalis by Chung (1931). In *Pseudosalamandra*, *Hynobius tsushimensis* and *H. leechii* (Chung, 1931), as well as in *Onychodactylus japonicus* (Ryke, 1950), this incisure is confluent with the fenestra lateralis nasi. Chung (1931), however, claims that in the latter species the incisura is distinct from the fenestra lateralis nasi. This discrepancy might be attributable to a difference in the ages of the specimens examined. In *Pseudotriton ruber ruber* Seydel's palatal process is very small, so that there is only a mere indication of the incisura ectochoanalis (fig. 2).

The choana lies in the posterior part of the fenestra endochoanalis.

Topographically the planum conchale is the backward continuation of the cartilago obliqua (fig. 1). On the anterior, dorsal surface of the planum conchale there is a groove, the impressio conchalis (external nasolacrima groove, Jarvik, 1942) in which runs the anterior part of the nasolacrima duct just before it enters the fenestra narina. The impressio conchalis is matched on the under surface of the planum by the crista rostrocaudalis. De Beer (1937) regards it as an exceedingly rudimentary concha nasalis. It is entirely absent in *Diemictylus* (Chung, 1931). Both planum conchale and impressio conchalis are absent in *Ambystoma tigrinum* (Grote, 1926).

The planum conchale merges posteriorly into the cartilago antorbitalis, which separates the nasal cavity and the orbit from each other. Postero-laterally the cartilago antorbitalis forms a backward extension, the processus maxillaris posterior, which lies in a groove in the maxillary (figs. 1 and 2). In the cartilago antorbitalis there are two orbitonasal foramina which De Beer (1937) regards as indicative of the boundary line between the lamina orbitonasalis and the pre-optic root of the orbital cartilage.

The foramen orbitonasale mediale is situated laterally to the foramen olfactorium in the medial part of the cartilago antorbitalis (fig. 1). The ramus medialis nasi V(a) and the ramus ventralis nasi V(a) pass through the foramen orbitonasale mediale from the orbit into the cavum nasi. The r. medialis nasi V(a) and a bloodvessel pass through the dorsal portion of the foramen, while the r. ventralis nasi V(a) passes through its ventral portion. The r. ventralis nasi V(a) eventually joins the r. palatinus VII at the ganglion palatinum, and from there



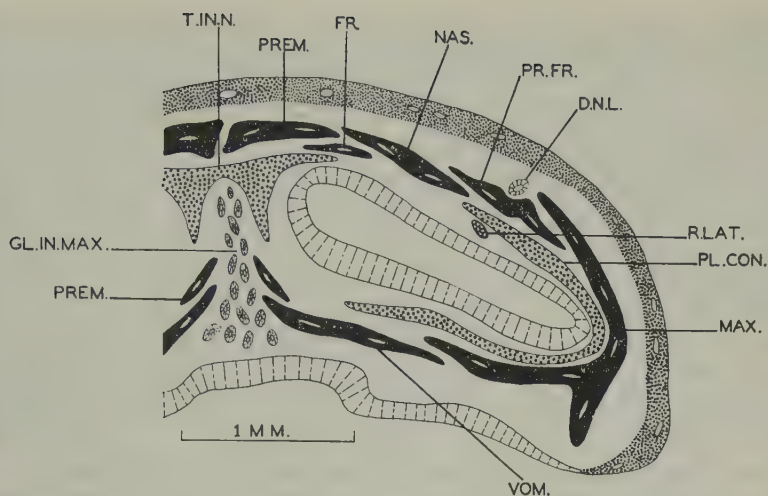


Figure 4.

Transverse section through the region of the planum conchale. D.N.L. ductus nasolacrimalis; FR. frontal; GL.IN.MAX. glandula intermaxillaris; MAX. maxillary; NAS. nasal; PL.CON. planum conchale; PREM. premaxillary; PR.FR. prefrontal; R.LAT. ramus lateralis nasi V(a); T.IN.N. tectum internasale; VOM. vomer.

nerve fibres of the combined nerve stretch anteriorly, medially to the choana and dorsally to the vomer. The foramen orbitonasale laterale is situated antero-laterally to the foramen orbitonasale mediale (fig. 1). Through it the ramus lateralis nasi V(a) enters the cavum nasi (fig. 5).

The r. medialis nasi V(a) leaves the cavum nasi by the foramen apicale which is situated antero-dorsally in the columella ethmoidalis (fig. 1). Chung (1931) found a similarly situated foramen apicale in *Onychodactylus*, *Hynobius*, *Diemictylus* and *Pseudosalamandra*. In *Salamandra* (Stadtmüller, 1930) the foramen apicale lies ventrally to the processus praenasalis inferior lateralis. Jarvik (1942) maintains that it is impossible to establish the homology of the foramen apicale, as its position in the *Urodela* varies considerably.

## THE MEMBRANE BONES OF THE OLFACTORY REGION

The premaxillaries are completely fused anteriorly (figs. 1 and 2), a condition corresponding to that in *Triturus* (Gaupp, 1906). In *Megalobatrachus* (Aoyama, 1930), *Ambystoma tigrinum* (Grote, 1926), *Onychodactylus* (Ryke, 1950), *A. maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the premaxillaries are separate. Each premaxillary consists of the following clearly recognisable parts: a processus praenasalis (frontalis), a pars dentalis and a pars palatina. Posteriorly the long, postero-dorsally directed processus praenasalis is in close contact with its partner of the other side, but the anterior parts of these processes diverge somewhat, so that the cavum internasale is incompletely covered antero-dorsally (fig. 1). Immediately behind

the region of fusion of the partes dentales each processus praenasalis extends upwards and backwards. Its posterior end overlaps the frontal to a certain extent, whereas its antero-lateral part is overlain by the nasal (fig. 1). In *Salamandra* (Francis, 1934) the processus praenasalis overlaps the nasal and the frontal, whereas in *Onychodactylus* (Ryke, 1950) it overlaps the anterior portion of the nasal only. From Theron's (1952) figures it is clear that the processus praenasalis has no contact with the nasal in *Ambystoma maculatum*, while Papendieck (1954) states that it does not overlap the nasal in *A. macrodactylum*; in both cases it overlaps the anterior portion of the frontal only. The processus praenasalis is better developed in the higher urodeles than in the more primitive ones: long in the *Salamandridae* and *Ambystomidae*, and short in the *Hynobiidae* and *Cryptobranchidae*. Jarvik (1942) is therefore of opinion that the processus praenasalis has undergone progressive development in the *Urodela*. Laterally, the antero-ventrally situated pars dentalis is in close contact with the maxillary (fig. 2). The pars palatina, which forms the bony palate, is well developed, as in *Salamandra* (Francis, 1934). In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the pars palatina is very poorly developed, and it is entirely absent in *A. tigrinum* (Grote, 1926). The pars palatina is underlain by the vomer (figs. 2, 3 and 4).

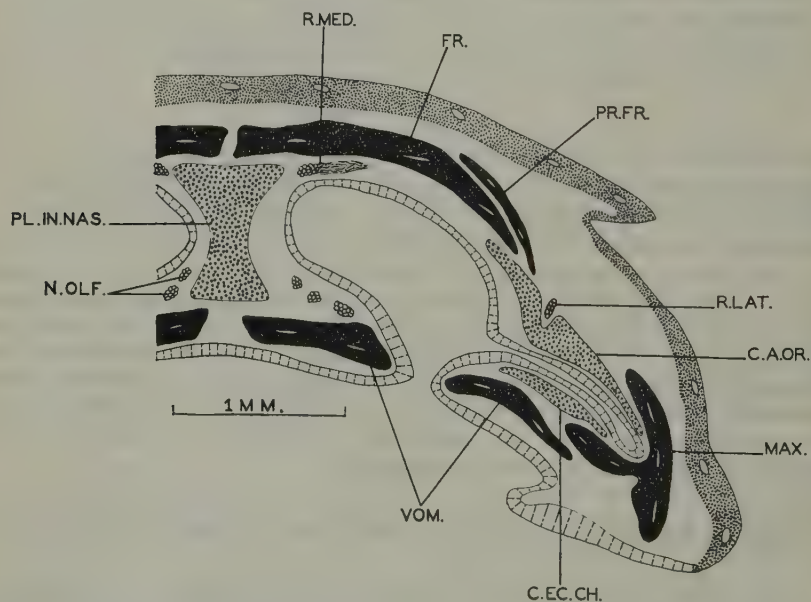


Figure 5.

Transverse section showing the planum internasale. C.A.OR. cartilago antorbitalis; C.EC.CH. cartilago ectochoanalis; FR. frontal; MAX. maxillary; N.OLF. nervus olfactorius; PL.IN.NAS. planum internasale; PR.FR. prefrontal; R.LAT. ramus lateralis nasi V(a); R.MED. ramus medialis nasi V(a); VOM. vomer.

Each maxillary consists of a pars dentalis, a pars facialis and a pars palatina, all of which are strongly developed. The pars palatina is antero-medially underlain by the vomer (figs. 2, 3, 4 and 5). The pars



palatina of *Salamandra* (Francis, 1934) reaches the vomer, whereas it fails to do so in *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). The pars dentalis is comparatively large and its backward extension, the processus maxillaris posterior, reaches into the orbit. Its posterior tip lies antero-laterally to the processus pterygoideus (figs. 1 and 2). The dentary part of the maxillary has in this region a shallow groove, in which lies the processus maxillaris posterior of the cartilago antorbitalis (fig. 1). In *Salamandra* (Francis, 1934), *Onychodactylus* (Ryke, 1950) and *Ambystoma macrodactylum* (Papendieck, 1954) the maxillary does not reach the processus pterygoideus. In *Ambystoma maculatum* (Theron, 1952) the anterior part of the processus pterygoideus overlies the posterior tip of the maxillary, the two structures being connected by ligaments only. The pars facialis overlaps the prefrontal antero-laterally (figs. 1 and 4). The fenestra lateralis nasi is completely covered by this part of the maxillary.

The large, triangular vomer covers the fenestra basalis nasi and nearly the whole nasal capsule ventrally (fig. 2), though not as completely as in *Salamandra* (Francis, 1934). The vomer underlies the palatal parts of both premaxillary and maxillary (figs. 2, 3, 4 and 5). Posteriorly it underlies the anterior tip of the parasphenoid (figs. 2 and 6). In *Megalobatrachus* (Aoyama, 1930) and *Salamandra* (Francis, 1934) the vomer articulates laterally with the premaxillary and with the maxillary, but in *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) this is not the case, as the palatal parts of these bones and the vomer do not make contact. In the specimens examined, the vomers lie near each other, and the anterior palatal fenestra (Jarvik, 1942) is, therefore, very small (fig. 2). In *Salamandra* (Francis, 1934), *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the vomers are anteriorly far apart, thus leaving the cavum internasale completely devoid of a dermal floor. In the above-mentioned species there is a large anterior palatal fenestra. In *Triturus* (Wiedersheim, 1877), however, the vomers are suturally connected over nearly their whole length and the anterior palatal fenestra is represented by a small foramen only. This condition is regarded as secondary, as the cavum internasale of the *Porolepiformes* and primitive urodeles is wide open ventrally (Jarvik, 1942). A deep incisure cuts into the postero-lateral part of the vomer dividing it incompletely into broad, flat anterior and narrow, laterally projecting, posterior portions between which the choana is situated (fig. 2). The hinder portion of the vomer is tooth-bearing. In each vomer there is an antero-medially situated foramen (fig. 2) transmitting a bloodvessel and nerve fibres of the combined ramus ventralis nasi V(a) and r. palatinus VII supplying the dorsal epithelium of the buccal cavity.

A palatine is absent, and this condition is probably similar to that in *Megalobatrachus* (Aoyama, 1930) where a palatine is present in the larval stage but disappears during metamorphosis. Another possibility is that during the ontogeny the palatine has fused with the vomer, thus giving rise to a vomero-palatine (Stadtmüller, 1936).

The anterior portion of the fenestra dorsalis nasi is incompletely covered by the broad, flat nasal, the postero-lateral part of which is covered by the prefrontal, whereas its posterior part is underlain by the frontal (fig. 1). Its antero-median part overlaps the processus praenasalis of the premaxillary (fig. 1), as is the case in *Salamandra*

(Francis, 1934). In *Onychodactylus* (Ryke, 1950), on the other hand, the processus praenasalis of the premaxillary overlaps the anterior portion of the nasal. In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the nasal does not overlap the processus praenasalis of the premaxillary. In the specimens examined, the nasal does not take part in the skeletal support of the external nasal aperture, as it does in *Salamandra* (Francis, 1934). Antero-medially the nasal has two foramina for the transmission of the branches of the ramus medialis nasi V(a) (fig. 1).

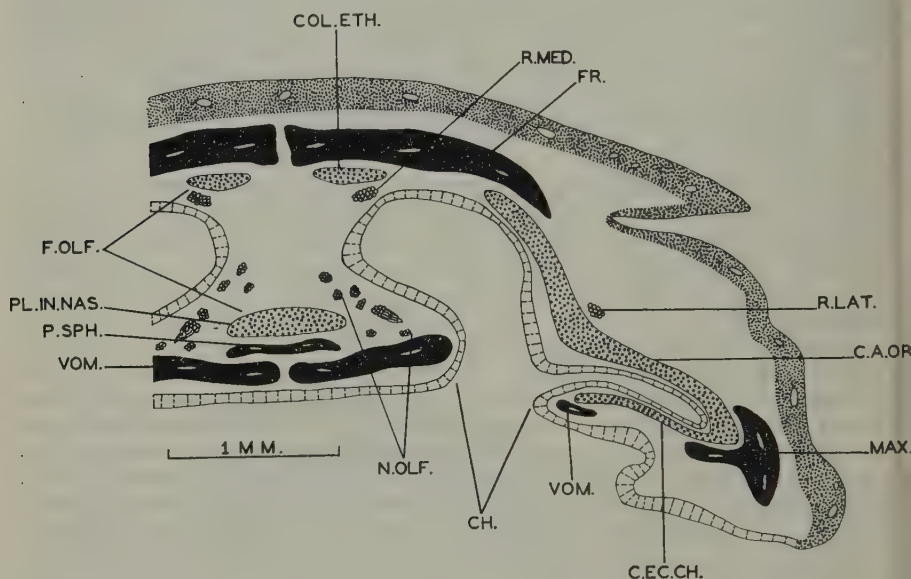


Figure 6.

Transverse section through the foramen olfactorium. C.A.OR. cartilago antorbitalis; C.EC.CH. cartilago ectochoanalis; CH. choana; COL.ETH. columella ethmoidalis; F.OLF. foramen olfactorium; FR. frontal; MAX. maxillary; N.OLF. nervus olfactorius; PL.IN.NAS. planum internasale; P.SPH. paraspheoid; R.LAT. ramus lateralis nasi V(a); R.MED. ramus medialis nasi V(a); VOM. vomer.

The flat prefrontal is the only circumorbital membrane bone, a lacrimal being absent (fig. 1). The prefrontal covers the posterior portion of the fenestra dorsalis nasi and overlaps the postero-lateral part of the nasal; it is itself overlapped laterally by the pars facialis of the maxillary (fig. 1). Postero-medially it overlaps the anterior portion of the frontal. Anteriorly the prefrontal is pierced by the ductus nasolacrimalis as in *Triturus* (De Beer, 1937), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). Jarvik (1942) regards this condition as secondary. According to Stadtmüller (1936) the prefrontal is absent in *Proteus* and in *Necturus*. Gregory (1920) states that in most urodeles the lacrimal has disappeared. A lacrimal is present in *Gyrinophilus* (Cope, 1889), *Ranodon* and *Hynobius* (s. *Ellipsoglossa*) (P. and F. Sarasin, 1890) and *Onychodactylus* (Chung, 1931; Ryke, 1950), but De Beer (1937) states that it may have fused with the prefrontal. Papendieck (1954) regards it as



highly probable that in *Ambystoma macrodactylum* the lacrimal is fused with the prefrontal. As I did not have any ontogenetic material at my disposal, it is difficult to decide whether the prefrontal of *Pseudotriton ruber ruber* represents a mixed bone or whether the lacrimal has simply been lost.

The septomaxillary (nariodal, Jarvik, 1942) is a small bone situated in the posterior part of the fenestra narina (fig. 1). It surrounds the ductus nasolacimalis dorsally, medially and laterally. At the moment there is still some uncertainty about the nature of the septomaxillary. Lapage (1928), Chung (1929) and Jarvik (1942) regard it as a cartilage bone. If we accept their statements, it would mean that the septomaxillary of the *Urodela* is not homologous with the septomaxillary of forms in which it has definitely been proved to have a membranous origin. Barry (1956a) maintains that in *Bufo angusticeps* the septomaxillary has a membranous origin, and points out that Lapage's (1928) statements cannot be accepted, as the stages investigated by her did not include material young enough to supply evidence for the origin of the septomaxillary in the *Anura*. Hasurkar (1958) working on *Rana tigrina* also found that the septomaxillary has a membranous origin. In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the septomaxillary is separated from the nasal cartilage by connective tissue; this is additional proof of the membranous origin.

In the specimens I examined, the septomaxillary is anteriorly separated from the nasal cartilage by connective tissue, but more posteriorly it is continuous with the nasal cartilage. The bone invades the cartilage, thus simulating perichondral ossification of the latter. Owing to the lack of ontogenetic material, I hesitate to venture an opinion on this matter, as in this case it seems possible that the septomaxillary represents a mixed bone. Schmalhausen (1958) maintains that the septomaxillary has a membranous origin, but that it may become closely apposed to the cartilage of the nasal capsule in the older developmental stages of the *Hynobiidae*. This author suggests that the septomaxillary is homologous with the dermal bone transmitting the subnasal part of the canalis infra-orbitalis in the *Osteichthyes*. His contention is that the urodelous septomaxillary is homologous with that found in the anurans and in the reptiles.

A septomaxillary is present in *Desmognathus* and *Plethodon* (Lapage, 1928), *Hynobius* (Chung, 1929), *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954), but it is lacking in *Salamandra*, *Amphiuma* and *Necturus* (Lapage, 1928), *Diemictylus* (Chung, 1929), *Megalobatrachus* (Aoyama, 1930) and *Proteus* and *Siren* (Stadtmüller, 1936).

## THE ORBITO-TEMPORAL REGION

In this region the chondrocranium consists of a pair of horizontal, medially concave lamellae forming the side-walls of the brain-case (figs. 1 and 2). There is no roof and ventrally there is a large fenestra basiscranialis communis bordered posteriorly by the hypochordal commissure (fig. 2).

The orbitosphenoid is the anterior ossification of the side-wall of the brain-case (figs. 1 and 2). It stretches from the cartilago antorbitalis to approximately the middle of the foramen oculomotorium (fig. 2). The

foramen opticum lies completely within the orbitosphenoid (fig. 2), which therefore, includes not only the preoptic root of the orbital cartilage, but the pila metoptica as well. A similar condition obtains in *Salamandra* (Stadtmüller, 1924; Francis, 1934) and *Megalobatrachus* (Aoyama, 1930). In *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) only the anterior portion of the foramen opticum is situated in the orbitosphenoid, its hinder border being formed by the posterior continuation of the cartilaginous side-wall of the brain-case. The foramen opticum is much larger than the nervus opticus, connective tissue intervening between it and the bony border of the foramen.

Immediately behind the foramen opticum, there is the much smaller foramen oculomotorium (fig. 2) transmitting the nervus oculomotorius and the arteria ophthalmica. In *Onychodactylus* (Ryke, 1950) the arteria ophthalmica has its own foramen, called the foramen ophthalmicum.

The foramen prooticum is situated between the cartilaginous side-wall of the brain-case and the anterior end of the otic capsule (fig. 2). It is separated from the foramen oculomotorium by the pila antotica. In the foramen prooticum lies the ganglion Gasseri and through it pass the nervus trigeminus, the nervus abducens and a bloodvessel. In *Salamandra* (Francis, 1934) and *Onychodactylus* (Ryke, 1950) the nervus abducens leaves the cavum cranii by its own foramen, the foramen abducentis. In *Pseudotriton ruber ruber* the nervus abducens is closely associated with the ganglion Gasseri and leaves the cranial cavity together with the nervus trigeminus, on the posterior side of the latter.

Aoyama (1930) found a foramen trochleare in the side-wall of the brain-case of *Megalobatrachus*, through which the nervus trochlearis passes. This foramen is not present in the specimens examined by me, as the nervus trochlearis pierces the parietal.

The arteria carotis interna leaves the cranial cavity medially to the foramen prooticum, and runs in a groove on the ventral, internal surface of the lateral wall of the cranial cavity. This groove, the carotid canal, is ventrally covered by the parasphenoid. The arteria carotis interna enters the cavum cranii through the fenestra basicranialis communis.

A sclerotic cartilage is completely lacking. According to Stadtmüller (1914) and Okajima and Tsusaki (1921), the sclera of the adults of some primitive urodeles, as well as the larvae of most forms, is strengthened by a ring or cup of cartilage.

## THE MEMBRANE BONES OF THE ORBITO-TEMPORAL REGION

The paired frontals are the large, flat bones covering the anterior portion of the cranial cavity and, to a large extent, the posterior portion of the fenestra dorsalis nasi (fig. 1). The posterior end of each frontal is bluntly rounded; posteriorly it overlaps a considerable portion of the parietal. Anteriorly each frontal is overlapped by the processus praenasalis of the premaxillary, by the nasal, and antero-laterally by the prefrontal (fig. 1).

The dermal roof of the posterior portion of the cranial cavity is formed by the large parietals, which extend backwards into the otic region and overlap the anterior portion of the otic capsules (fig. 1).



Each parietal has a latero-ventrally directed processus orbitalis (Wiedersheim, 1877) pierced by the foramen trochleare. In *Ambystoma opacum* (Parker, 1877) and *A. maculatum* (Theron, 1952) the parietal has a lateral crest roofing a fossa in which a muscle is attached.

The large, unpaired, tooth-bearing parasphenoid forms the dermal floor of the cranial cavity. It covers the large fenestra basicranialis communis ventrally (fig. 2). Its anterior tip lies dorsally to the vomer and it stretches from a point a little behind the cavum internasale to the occipital region; its hind end narrows and ends bluntly rounded (fig. 2). The parasphenoid is separated from other structures by connective tissue.

## THE OTIC AND OCCIPITAL REGIONS

The prootic and the exoccipital are indistinguishably fused to form a prootic-exoccipital complex (figs. 1 and 2), which Stadtmüller (1936) named the os occipito-petrosum. Residual cartilage, representing the cartilago prootico-occipitalis, occurs ventrally and completely surrounds the fenestra ovalis (fig. 2). Stadtmüller (1936) states that fusion of the prootic and exoccipital occurs in most urodeles and some anurans. In *Onychodactylus* (Ryke, 1950) the two bones in question are fused dorso-laterally, but on the ventral and medial sides they are separated by narrow strips of cartilage, the cartilago prootico-occipitalis. In *Desmognathus* and *Dicamptodon* (Stadtmüller, 1936) synostosis exists between the parasphenoid and the prootic. The otic capsules are dorsally connected by the cartilaginous tectum synoticum (fig. 1). Ventrally the otic capsules are connected by the hypochordal commissure (fig. 2).

Since a crista sellaris and a fenestra basicranialis posterior are absent, a large fenestra basicranialis communis is present. A similar condition is found in *Diemictylus*, *Plethodon* and *Desmognathus* (Stadtmüller, 1936) in which the crista sellaris has undergone resorption. In *Megalobatrachus* (Aoyama, 1930) a fenestra basicranialis posterior never occurs, not even in the larvae. According to De Beer (1937) it develops in *Necturus*, but the crista sellaris later undergoes resorption so that the fenestra basicranialis posterior becomes confluent with the fenestra basicranialis anterior. Winslow (1898) reports that the larval *Amphiuma* has two fenestrae basicraniales posteriores, which, owing to the resorption of the crista sellaris and the flanking cartilage of the notochord, are later united with the fenestra basicranialis anterior, thus forming a fenestra basicranialis communis. Stadtmüller (1936) claims that in *Salamandra*, and in others, in which the fenestra basicranialis posterior is absent during the early stages of ontogeny, a secondary fenestra is formed in the basal plate through resorption of cartilage. In the majority of urodeles a fenestra basicranialis posterior is present. It varies in size and in *Onychodactylus* (Ryke, 1950) it is a mere slit. In *Ambystoma macrodactylum* (Papendieck, 1954) there are two fenestrae basicraniales posteriores; a unique circumstance which Papendieck ascribes to neoteny. Vestiges of the notochord in this region of the skull are reported for *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954), but in the specimens examined by me, no traces of the notochord could be found.

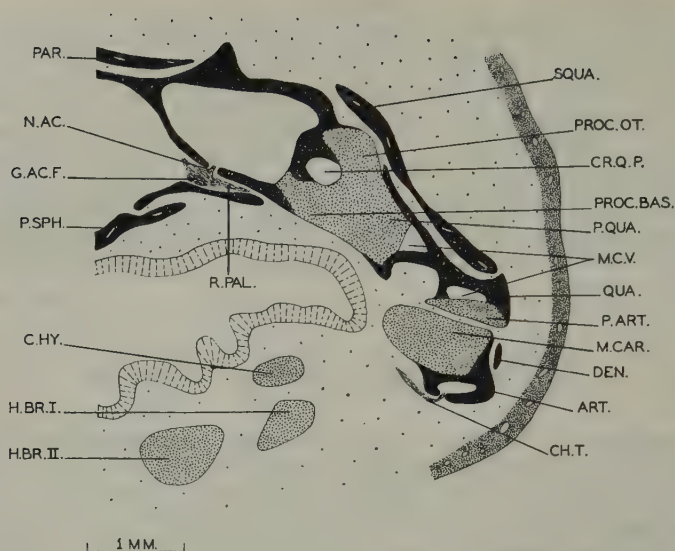


Figure 7.

Transverse section through the region of the processus oticus and processus basalis. ART. articular; CH.T. chorda tympani; C.HY. ceratohyal; CR.Q.P. cranio-quadrate passage; DEN. dentary; G.A.C.F. ganglion acustico-faciale; H.BR.I. hypobranchial I; H.BR.II. hypobranchial II; M.CAR. Meckel's cartilage; M.C.V. marrow cavity; N.AC. nervus acusticus; PAR. parietal; P.ART. pars articularis; P.QUA. pars quadrata; PROC.BAS. processus basalis; PROC.OT. processus oticus; P.SPH. parasphenoid; QUA. quadrate; R.PAL. ramus palatinus VII; SQUA. squamosal.

The cartilaginous processus basiptyergoideus is fused to the antero-ventral portion of the otic capsule, which possesses a dorso-lateral ridge serving as a support for the squamosal. A similar ridge is found in *Ambystoma gracile* (Eaton, 1933), *A. maculatum* (Theron, 1952), *A. macrodactylum* (Papendieck, 1954) and *Hynobius retardatus* and *H. nebulosus* (Fox, 1959), but it is absent in *Rhyacotriton* (Eaton, 1933).

The medial wall of the otic capsule is completely ossified and is pierced by a number of foramina. The medial wall in this region remains membranous in *Triturus* (De Beer, 1937). The ganglion acustico-faciale (fig. 7) is housed partly in the recessus acustico-facialis, situated antero-ventrally in the otic capsule. There is no intracranial ramus communicans connecting the ganglion acustico-faciale to the ganglion Gasserii, as reported by some authors for *Ambystoma* spp.

Laterally to the ganglion acustico-faciale both the ramus palatinus VII and the ramus hyomandibularis VII run in the facial canal, the roof of which is formed by the floor of the otic capsule. The facial canal opens distally through the palatine foramen transmitting the palatine branch (figs. 2 and 7), whereas more posteriorly the hyomandibular branch leaves the canal through its own foramen leading into the cranio-quadrate passage. The foramen acusticum is situated

immediately dorsally to the ganglion acustico-faciale, and it is through this single foramen which the branches of the nervus acusticus enter the otic cavity (fig. 7). Dorsally to this foramen and slightly farther back, there is a foramen in the medial wall of the otic capsule for the passage of the ductus endolymphaticus. More posteriorly and ventrally, it has another foramen for the transmission of the ductus perilymphaticus.

The nervus glossopharyngeus and the nervus vagus pass through a single foramen, the foramen postoticum, situated in the prootic-exoccipital complex, immediately behind the otic capsule and dorsally to the condylus occipitalis (fig. 1). The comparatively large fenestra ovalis is situated in the postero-lateral surface of the otic capsule, and is surrounded by the cartilago prootico-occipitalis (figs. 2 and 8).

## THE SOUND-CONDUCTING APPARATUS

The sound-conducting apparatus consists of two structures, the "columella" and the operculum; the latter is fused to the footplate of the former. According to Eiselt (1941) this is the case in the *Amphiumidae*, *Plethodontidae* and *Proteidae*, whereas Stadtmüller (1936) merely states that this fusion is the rule in all plethodontids and desmognatids, both of which have since been incorporated in the family *Plethodontidae*. This fused structure fits into the fenestra ovalis, which, surrounded by residual cartilage, is situated in the postero-lateral wall of the otic capsule (figs. 2 and 8). The sound-conducting apparatus is postero-ventrally in synchondrotic connexion with the residual cartilage and elsewhere it is in syndesmosis with it (fig. 8). The significance of this fusion will be dealt with later. Perichondral ossification occurs over the whole structure, excepting the stylus columellae which remains unossified (figs. 2 and 8). In *Salamandra* (Francis, 1934), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the sound-conducting apparatus consists of two independent structures, a columella and an operculum. According to Barry (1956b) the operculum, as a separate entity, is only found in the anurans and urodeles. The footplate of the columella in *Onychodactylus* (Ryke, 1950) is fused to the anterior wall of the fenestra ovalis, and shows signs of perichondral ossification. Fusion of the columella to the otic capsule is also found in *Rhyacotriton* (De Villiers, 1938), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). Eiselt (1941) states that the columella is fused to the otic capsule in the *Ambystomidae*, *Salamandridae* and *Sirenidae*. The columella remains free in *Hynobius* and in *Cryptobranchus* (Dunn, 1922).

The lateral, distal portion of the stylus columellae is in syndesmotic connexion with the dorsal tip of the quadratojugal (fig. 2). In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the stylus columellae is connected to the pars quadrata palatoquadrati by the ligamentum suspensorio-columellare. In *Salamandra* (De Beer, 1937), *Rhyacotriton* (De Villiers, 1938) and *Onychodactylus* (Ryke, 1950) this connexion is synchondrotic. In *Megalobatrachus* (Aoyama, 1930) this synchondrosis exists only in the larvae, but is absent in the adults.

Reinbach (1950) regards the columella as arising partly from the otic capsule and partly from the pars quadrata, so that a connexion



with the latter must be of a primary nature. Kingsbury and Reed (1908) consider this connexion as secondary. The ontogenetical studies of Barry (1956b) and Van der Westhuizen (in press) on *Bufo* and *Heleophryne* respectively, lend support to Reinbach's theory. Reinbach (1950) is of opinion that the urodelous columella consists of a pars media columellae and a pars interna columellae, comparable with those of the anurans, but that it lacks a pars externa columellae. He claims that in urodeles the pars interna develops from the otic capsule, and the pars media from the pars quadrata palatoquadrati. As the two parts constituting the urodelous columella originate from two different sources, he suggests that the pars interna be called the pars otica columellae, and the pars media the pars quadrata columellae.

The ramus hyomandibularis VII (fig. 8) runs ventrally to and in front of the laterally projecting stylus columellae, which separates the vena capitis lateralis from its branches; the main branch running ventrally to the stylus columellae (fig. 8).

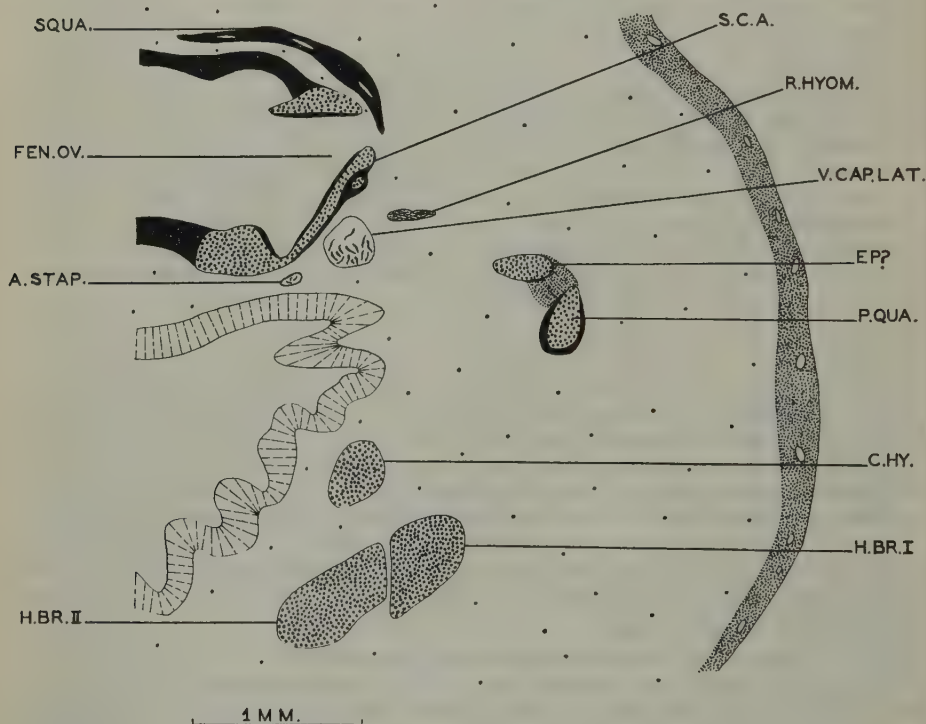


Figure 8.

Transverse section through the fenestra ovalis. A.STAP. arteria stapedialis; C.HY. ceratohyal; EP. epihyal; FEN.OV. fenestra ovalis; H.BR.I. hypobranchial I; H.BR.II. hypobranchial II; P.QUA. pars quadrata; R.HYOM. ramus hyomandibularis; S.C.A. sound-conducting apparatus; SQUA. squamosal; V.CAP.LAT. vena capitis lateralis.

According to Eiselt (1941) the opercular muscle can originate only from the operculum, or by inference, from the opercular moiety of a fused operculum and a columella footplate (cf. Kingsbury and Reed, 1909). This view is corroborated by Dunn (1941) according to whom an opercular muscle is absent in forms lacking an operculum, such as *Amphiuma* and *Rhyacotriton*. The circumstance that in *Pseudotriton* the opercular muscle stretches between the suprascapula and the posterior proximal portion of the sound-conducting apparatus clearly indicates that an operculum is fused with the footplate of the columella.

The footplate is apparently not of visceral origin since Iwanzoff (1894), Fuchs (1907), Kingsbury and Reed (1909), Reinbach (1950) and Schmalhausen (1956) state that it arises from cells liberated from the otic capsule. Barry (1956b) states that in *Bufo angusticeps* the operculum is mainly of capsular origin, but that it might also be partly formed from the basal plate. Van der Westhuizen (in press) claims that in *Heleophryne purcelli* the operculum develops from cells liberated mainly from the ventral rim of the fenestra ovalis. Iwanzoff (1894) maintains that the columella has nothing in common with the operculum, although the two structures in question are sometimes fused.

"There can no longer be any reasonable doubt that the operculum of the *Anura* is homologous with that of the *Urodela*. It occupies the same position in the posterior portion of the fenestra ovalis, it affords attachment to the same muscle, the musculus opercularis, and its mode of development appears to be similar in both these amphibian orders" (Van der Westhuizen, in press). This author also maintains that the cartilaginous connexion of the operculum with the dorsal rim of the fenestra ovalis is secondary in *Heleophryne*. As the operculum in the anurans and in the urodeles apparently develops in the same way, the cartilaginous connexion of the opercular portion of the sound-conducting apparatus with the ventral rim of the fenestra ovalis in *Pseudotriton* must be considered primary. Schmalhausen (1957) claims that the operculum and the musculus opercularis are not part of the sound-conducting apparatus, but probably function as an accommodation apparatus. Eiselt (1941) declares: "Der M. opercularis und das Operculum arbeiten als Bewegungskorrelations- und nicht, wie früher angenommen wurde, als Vibrationsleitungsorgan" (p. 213).

In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) there is a slight synchondrotic connexion between the operculum and the dorsal rim of the fenestra ovalis. In *Hynobius* (Dunn, 1922), *Salamandra* (Francis, 1934) and *Triturus* (De Beer, 1937) the operculum has no such connexion. An operculum is absent in *Cryptobranchus* and *Necturus* (Kingsbury and Reed, 1909), *Megalobatrachus* (Aoyama, 1930), *Amphiuma* (De Beer, 1937), *Rhyacotriton* (Dunn, 1941) and *Onychodactylus* (Ryke, 1950). According to Kingsbury and Reed (1909) the operculum has developed as an adaptation to terrestrial life and both it and the accompanying muscle are absent in the aquatic larval stages. Piatt (1938), however, found a weakly developed musculus opercularis in larval *Ambystoma*.

## THE PALATOQUADRATE AND SUSPENSORIUM

The anterior tip of the processus pterygoideus lies postero-medially to the posterior tip of the maxillary and is entirely free (figs. 1 and 2). In *Ambystoma maculatum* (Theron, 1952) it overlaps the posterior portion of the maxillary, but in *A. macrodactylum* (Papen-

dieck, 1954) it "ends a short distance behind this bone" (p. 168). In *Onychodactylus* (Ryke, 1950) it lies medially to the posterior tip of the maxillary, but does not touch it. The pars quadrata lies ventro-laterally to the otic capsule and is connected to the neurocranium by the processus ascendens, processus basalis and the processus oticus. A cranio-quadrata passage is thus formed, through which pass the ramus hyomandibularis VII and the vena capitis lateralis. Similar conditions exist in *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). The arteria stapediales pass ventrally to the processus basalis.

The processus ascendens (fig. 1) stretches from the anterior portion of the pars quadrata in an antero-medio-dorsal direction and is in synchondrotic union with the cartilaginous side-wall (pila antotica) of the neurocranium. Similar conditions obtain in *Salamandra* (Francis, 1934), *Rhyacotriton* (De Villiers, 1938), *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). The ganglion Gasseri is situated medially to the processus ascendens, and normal conditions exist regarding the relation of the branches of the nervus trigeminus. Francis (1934) describes perichondral ossification in the processus ascendens of *Salamandra*; a condition which was confirmed by Stadtmüller (1936).

The cartilaginous processus oticus (figs. 1 and 7) is situated further back, parallel to the processus ascendens and is fused to the crista parotica. It lies antero-laterally to the ramus hyomandibularis VII and dorso-laterally to the vena capitis lateralis. Similar conditions are encountered in *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). Only traces of a vestigial processus oticus are present in *Rhyacotriton* (De Villiers, 1938).

The processus basalis is situated immediately below the processus oticus (fig. 7), borders the cranio-quadrata passage ventrally and is confluent with the processus basiptyergoideus. A similar synchondrosis is also found in *Diemictylus*, *Plethodon* and *Desmognathus* (Stadtmüller, 1936) and in *Triturus* and *Salamandra* (De Beer, 1937). The processus basalis in *Hynobius retardatus* and *H. nebulosus* (Fox, 1959), *Chioglossa* (Stadtmüller, 1936), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) has a diarthrosis with the basiptyergoid process, which, according to Gaupp (1906), is a primitive condition. In *Onychodactylus japonicus* Stadtmüller (1936) describes a diarthrosis on the one side and a synchondrosis on the other, while Ryke (1950) finds a differently developed diarthrosis on the two sides. The posterior tip of the pars quadrata is syndesmotically connected to the antero-dorso-laterally projecting portion of the ceratohyal of the hyobranchial apparatus (fig. 8). This part of the hyobranchial apparatus is topographically very much like that of *Rhyacotriton olympicus* (Cloete, in press). In the latter species this antero-dorso-laterally projecting portion could be identified as an epihyal, since it is histologically different from the adjoining structures. On purely topographical grounds it is tentatively suggested that the part of the hyobranchial apparatus of *Pseudotriton*, with which the pars quadrata is in syndesmosis, represents an epihyal. Whatever the true homology of this structure proves to be, the mere fact that the three processes of the pars quadrata are well developed, and that the hyoid arch partakes in the suspension of



the jaws, means that the jaw suspension of *Pseudotriton* is of the amphistylic type.

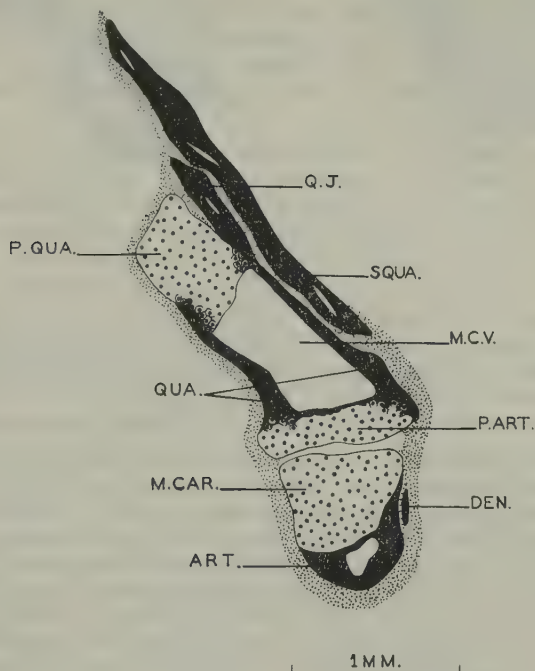


Figure 9.

Transverse section showing the fusion of the quadrate and the quadratojugal. ART. articular; DEN. dentary; M.CAR. Meckel's cartilage; M.C.V. marrow cavity; P.ART. pars articularis; P.QUA. pars quadrata; Q.J. quadratojugal; QUA. quadrate; SQUA. squamosal.

The quadrate, possessing a marrow cavity, is the sole ossification of the pars quadrata (figs. 7 and 9). Dorsally it is invaded by the quadratojugal, giving rise to a mixed bone (fig. 9).

The quadratojugal and the squamosal are the only membrane bones of the suspensorial region, and cover it dorso-laterally (figs. 7 and 9). A pterygoid is absent, as in *Siren* (Stadtmüller, 1936), whereas in *Hynobius* (De Villiers, 1936) it is fused to the quadrate. The quadratojugal consists of an upper portion, separated by connective tissue from the pars quadrata and the squamosal, and a lower portion which invades the quadrate dorsally (fig. 9). The squamosal, besides covering the suspensorial region dorso-laterally, also, to a certain extent, overlies the prootic-exoccipital complex (fig. 1). It is separated from all the other structures by connective tissue. In *Ambystoma opacum* (Wiedersheim, 1877) a synostosis exists between the squamosal and the quadrate.

Movement of the palatoquadrate is impossible, since the processus ascendens is fused to the chondrocranium, the processus oticus is synchondrotically connected to the crista parotica and the processus basalis and the neurocranium are confluent. The skull is, therefore, monimostylic and akinetic.

## THE LOWER JAW

The lower jaw has two membrane bones, the dentary and the gonial, the latter being medial to the former (figs. 10 a and b). They enclose a canal between them which contains Meckel's cartilage, a bloodvessel and nerve fibres. Gaupp (1911) named this canal the *canalis primordialis*.

Meckel's cartilage is a rod-like structure, the anterior end of which is ossified to form the mentomandibular, which is, however, indistinguishably fused with the dentary as in *Megalobatrachus* (Aoyama, 1930), *Onychodactylus* (Stadtmüller, 1936), *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). An unusual feature of the lower jaw of *Pseudotriton ruber ruber* is that the two mentomandibulars are fused with each other. A small strip of cartilage is, however, present in the posterior part of the symphysial region. The mentomandibular in *Ambystoma tigrinum* (Gaupp, 1911), however, remains independent. Papendieck (1954) found a marrow cavity in the mentomandibular-dentary complex of *Ambystoma macrodactylum*.

Posteriorly Meckel's cartilage gradually broadens and articulates with the pars articularis of the pars quadrata (figs. 7 and 9). Postero-ventrally it ossifies to form an articular (figs. 7 and 9), which is indistinguishably fused to the gonial, thus giving rise to a mixed bone, the gonio-articular. A similar fusion occurs in *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954). The articular is free in larval *Ambystoma tigrinum* and in *Salamandra*, but is absent in *Triturus alpestris* and in *Necturus maculatus* (Stadtmüller, 1936). In *Ambystoma opacum* (Stadtmüller, 1936) the articular fuses with both the dentary and the gonial, forming a mixed bone, the dento-gonio-articular.

The dentary is the larger of the two investing bones and is the only toothbearing bone of the lower jaw. Anteriorly it is fused with the mentomandibular and stretches backwards laterally to Meckel's cartilage almost to its posterior end (figs. 7, 9 and 10 a and b). Anteriorly its inner surface is deeply grooved and it almost completely encircles Meckel's cartilage, but more posteriorly the groove widens considerably. In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) the dentary is anteriorly pierced by a number of foramina dentofacialia, which transmit bloodvessels and cutaneous branches of the ramus mandibularis V. These foramina are absent in the specimens examined by me.

The gonial forms the medial border of the lower jaw and together with the dentary it encloses the *canalis primordialis*. In the posterior region the dorsal edges of these bones do not meet so that the canal becomes an open groove (figs. 10 a and b). The gonial, sharply pointed anteriorly, gradually broadens towards its posterior portion, expands medio-dorsally into a *processus coronoideus* (fig. 10 a) for the insertion of muscle fibres. Its ventral, posterior part, possessing a marrow cavity, invades the articular and the two marrow cavities merge into each other.

The ramus mandibularis V and the chorda tympani (r. alveolaris VII) are the two nerves associated with the lower jaw. The r. mandibularis V enters the *canalis primordialis* dorsally between the dentary and Meckel's cartilage (fig. 10 a) and extends forward for a short distance before leaving the canal ventrally by a slit in the gonial (fig. 10 b).

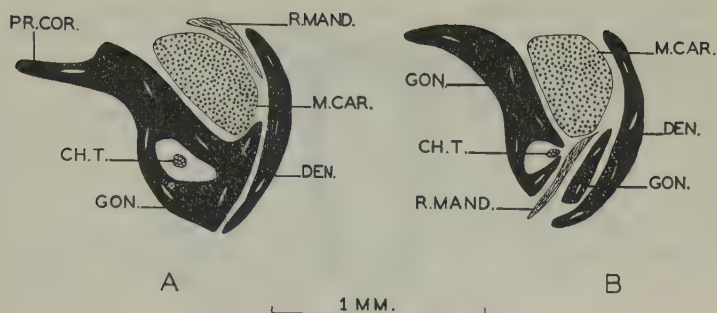


Figure 10 (a and b).

Transverse sections through the lower jaw to show the ramus mandibularis. CH.T. chorda tympani; DEN. dentary; GON. gonial; M.CAR. Meckel's cartilage; PR.COR. processus coronoidus; R.MAND. ramus mandibularis V.

The chorda tympani, after leaving the ganglion acustico-faciale, runs backwards ventrally to the ramus hyomandibularis VII and behind the stylus columellae it curves downwards and enters the marrow cavity of the articular through a foramen in its medio-ventral face (fig. 7). It proceeds forward in the marrow cavity for some distance and then enters the canalis primordialialis through a foramen situated in the medial wall of the slit in the gonial transmitting the r. mandibularis V (fig. 10 b). Gaupp (1911) states that the chorda tympani remains outside the canalis primordialialis in *Anura* and perennibranchiate *Urodela*, an observation which was confirmed by Hentschel (1936) for *Siren*.

### THE HYOBRANCHIAL APPARATUS

The hyoid arch is composed of two elements: a small hypohyal and a much larger ceratohyal (fig. 11). The hypohyal is represented by the rod-like radius anterior, as in *Salamandra* (Stadtmüller, 1936). Ventrally the radius anterior is synchondrotically connected to the anterior tip of the copula. A similar condition obtains in *Ambystoma macrodactylum* (Papendieck, 1954). In *Ambystoma maculatum* (Theron, 1952), however, this connexion is syndesmotic. The radius anterior, overlapping the anterior tip of the ceratohyal, stretches in an antero-dorso-lateral direction and ends freely as in *Salamandra* (Gaupp, 1904). In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) its outer end is attached to the ceratohyal by means of a strong ligament, a condition which is regarded as primitive (Gaupp, 1904). In *Onychodactylus* (Fukuda, 1930) the ceratohyal and the hypohyal are fused, whereas in *Triturus* (Gaupp, 1904) a hypohyal is absent.

The ceratohyal is a large, anteriorly broad and flat cartilage. It narrows considerably towards its hind end (fig. 11) which curves in an antero-dorso-lateral direction. This terminated portion becomes syndesmotically connected to the posterior tip of the pars quadrata (fig. 8). In the section dealing with the palatoquadrate and the suspensorium the possible homology of this terminal portion of the ceratohyal is discussed, and it is there suggested that it might represent an epihyal fused onto the ceratohyal.



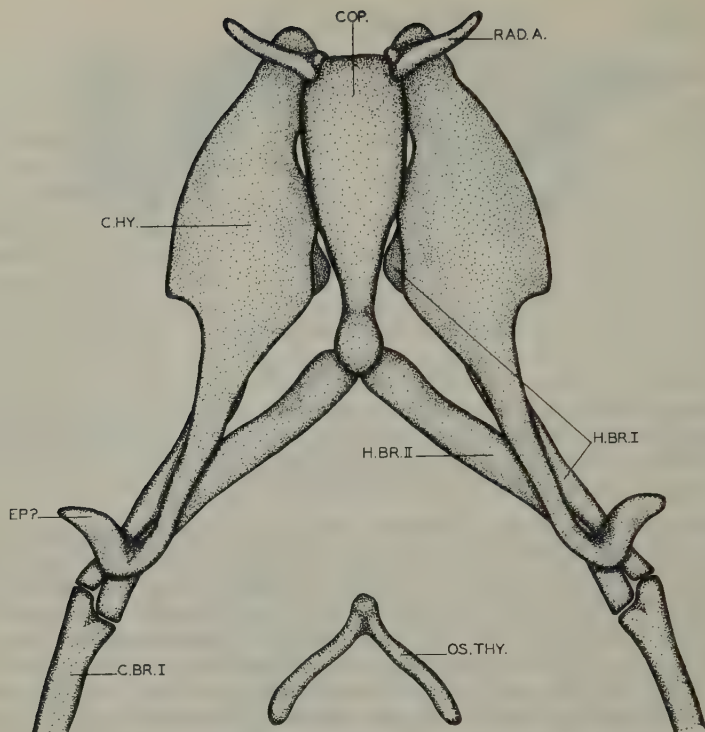


Figure 11.

Dorsal view of the hyobranchial apparatus  $\times 10.1$  approx. C.BR.I. ceratobranchial I; C.HY. ceratohyal; COP. copula; EP. epihyal; H.BR.I. hypobranchial I; H.BR.II. hypobranchial II; OS.THY. os thyroideum; RAD.A. radius anterior.

The copula (basibranchial, Wiedersheim, 1877) is the median, unpaired cartilage of the hyobranchial apparatus (fig. 11), with which the visceral arches are joined. In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) there are laterally projecting radii posteriores behind the radii anteriores which are in synchondrotic union with the copula. The two radii posteriores are dorsally connected by a cartilago arcuata. In the specimens examined by me, both the cartilago arcuata and the radii posteriores are lacking, whereas only the cartilago arcuata is absent in *Salamandra* (Francis, 1934). Radii posteriores are also lacking in *Triturus cristatus* and *T. taeniatus* (Gaupp, 1904) and *Hynobius* (Fox, 1959).

In *Pseudotriton ruber ruber* only the hypobranchials 1 and 11 and the ceratobranchial 1 are present (fig. 11). *Triturus cristatus* and *T. taeniatus* in addition possess a ceratobranchial 11 (Gaupp, 1904). The connexions between the branchial arches and the copula are weakly synchondrotic. A similar condition exists in *Ambystoma maculatum* (Theron, 1952). In *Ambystoma macrodactylum* (Papendieck, 1954) these connexions are syndesmotic. In *Salamandra* the first branchial arch consists of a narrow arcuate bar articulating with the copula on either side and comprising fused hypo- and ceratobranchial elements (Francis, 1934).

The os thyreoideum (fig. 11) is the bifurcated posterior portion of the larval copula-stalk, which remains after the copula-stalk disappears during metamorphosis (Gaupp, 1904). It is completely ossified in the specimens examined by me, but in *Ambystoma maculatum* (Theron, 1952) this structure is only anteriorly ossified, and in *A. macrodactylum* (Papendieck, 1954) it ossifies completely except for the posterior epiphyses which remain cartilaginous. In *Ambystoma maculatum* (Theron, 1952) the os thyreoideum lies immediately behind the copula and ventrally to hypobranchial 11. In the specimens examined and in *Salamandra* (Gaupp, 1904) and in *Ambystoma macrodactylum* (Papendieck, 1954), it is situated far more posteriorly.

## SUMMARY

- 1 A septum nasale is absent.
- 2 The glandula intermaxillaris is present and is situated in the cavum internasale.
- 3 The nasal capsules are joined by the tectum and planum internasale.
- 4 A processus praenasalis inferior lateralis, as well as an unpaired processus praenasalis superior medius, is lacking.
- 5 A fenestra praecerebralis is absent.
- 6 The fenestra lateralis nasi and the incisura ectochoanalis are separate.
- 7 The ductus nasolacimalis pierces the prefrontal anteriorly and enters the nasal capsule through the fenestra narina, behind the septomaxillary.
- 8 The premaxillaries are fused anteriorly.
- 9 The maxillary has dorsally a shallow groove in which lies the processus maxillaris posterior of the cartilago antorbitalis.
- 10 The vomer possesses an antero-medially situated foramen, transmitting a bloodvessel and nerve fibres of the combined ramus ventralis nasi V(a) and the r. palatinus VII.
- 11 The posterior part of the septomaxillary invades the cartilage bordering the fenestra narina.
- 12 A palatine is absent.
- 13 A sclerotic cartilage is lacking.
- 14 The foramen opticum is situated completely within the orbito-sphenoid, the latter reaching to approximately the middle of the foramen oculomotorium.
- 15 The nervus trochlearis pierces the processus orbitalis of the parietal.
- 16 The nervus trigeminus and the n. abducens both pass through the foramen prooticum.
- 17 The prootic and the exoccipital are fused, forming a prootic-exoccipital complex.
- 18 The ramus palatinus VII has its own foramen, the foramen palatinum.



- 19 Both the nervus glossopharyngeus and the n. vagus pass through the foramen postoticum.
- 20 A fenestra basicranialis communis is present.
- 21 The sound-conducting apparatus consists of a columella and an operculum; the latter is fused to the footplate of the former.
- 22 The opercular portion of the sound-conducting apparatus is in synchondrotic union with the ventral rim of the fenestra ovalis.
- 23 The stylus columellae is syndesmotically attached to the dorsal tip of the quadratojugal.
- 24 The musculus opercularis is well developed.
- 25 The processus ascendens is in synchondrotic union with the side-wall of the neurocranium.
- 26 The processus oticus is fused to the crista parotica.
- 27 The processus basalis is confluent with the processus basiptyergoideus.
- 28 The quadrate possesses a marrow cavity and is dorsally invaded by the quadratojugal.
- 29 An epihyal is probably present.
- 30 The skull is amphistylic; it is also monimostylic and akinetic owing to the immovability of the pars quadrata palatoquadrati.
- 31 The dentary and the gonial are the only membrane bones of the lower jaw.
- 32 The mentomandibular and the articular are the only cartilage bones of the lower jaw; the former is fused with the dentary and the latter with the gonial.
- 33 An unusual feature is that the two mentomandibulars are fused with each other.
- 34 The ramus mandibularis V leaves the canalis primordialialis through a slit in the gonial.
- 35 The radii posteriores and the cartilago arcuata are absent in the hyobranchial apparatus.

## DISCUSSION

It is generally accepted that the *Urodela* are a neotenic group; it is consequently extremely difficult to determine their relationship.

Apparently *Pseudotriton* is not neotenic at all, or only in one or two minor characteristics. It is a highly specialized genus, affording additional support to the view that the *Plethodontidae* are the most highly specialized family of the *Urodela*. *Pseudotriton* and *Gyrinophilus*, although highly specialized, are nevertheless the most primitive genera of the family.

The specialization of the *Plethodontidae* is confirmed by various characteristics of the skull of *Pseudotriton ruber ruber*, such as the reduction of the maxillaries, loss of the pterygoid and all circumorbital membrane bones except the prefrontal. (Loss of the pterygoid may perhaps be attributable to degeneration.) Furthermore, the operculum is fused to the footplate of the columella.

Although the skull is specialized in a number of features, it has also retained some primitive ones, such as the parasphenoid teeth. The retention of the parasphenoid teeth is, however, attributed by some authors to neoteny.

### ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Professor C. A. du Toit, under whose supervision this investigation was carried out, for his valuable advice, personal and continued interest in the progress of the work. I also wish to record my thanks to Professor C. G. S. de Villiers for his constructive criticism and to all the members of the staff of the Zoological Institute for their assistance.

I am also indebted to the Council for Scientific and Industrial Research for financial assistance, which enabled me to carry out these investigations.

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